

Seasonal changes in connectivity routes among larval fish assemblages in a semi-enclosed sea (Gulf of California)

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Seasonal changes in connectivity routes among larval fish assemblages in the northern Gulf of California were studied with connectivity matrices from particle-tracking with a 3D baroclinic numerical model. Results show strong seasonality in connectivity routes among assemblages according to the seasonal circulation phases. In summer (cyclonic phase), when circulation is dominated by the central cyclonic eddy and the northwestward coastal current on the mainland shelf, particle retention among assemblages after 30 days is high (>55%), and particle dispersion toward the Southern Gulf is low (<17%). Thus recruitment of most fish species must occur near their spawning areas: in June, coastal–demersal species such as *Gobulus crescentalis* and *Etropus crossotus*, and in August, coastal-epipelagic species such as *Opisthonema libertate* and species of the genus *Anchoa*. In winter (anticyclonic phase), when the coastal current is southeastward, particle retention among assemblages is low (<35%), and particle dispersion toward the southern gulf is high (>54%). Therefore, recruitment may occur away from the spawning locations, as suggested by the wide distribution of *Engraulis mordax* (coastal-epipelagic) and *Benthoosema panamense* (mesopelagic). Seasonal changes in connectivity routes show that ocean dynamics must be considered in management and conservation plans for marine ecosystems.

KEYWORDS: connectivity routes; larval fish assemblages; three-dimensional baroclinic model; Mexico; Gulf of California

INTRODUCTION

It is well recognized that circulation processes play an important role in zooplankton dispersion, including fish eggs and larvae, in the world oceans (e.g. Paris *et al.*, 2007). Mesoscale circulation may minimize long-distance dispersal by retaining or concentrating spawning products along features such as fronts (e.g. Cowen *et al.*, 2006; Leis, 2007). Studies of zooplankton

dispersion permit detection of potential spawning and recruitment areas of fish species, as well as connectivity routes (direction and distance) between areas, and their temporal changes (Fogarty and Botsford, 2007; Jones *et al.*, 2007).

In the last decade, studies focusing on zooplankton dispersal patterns and connectivity have increased (Cowen *et al.*, 2000; Hinrichsen *et al.*, 2003; Van der

Molen *et al.*, 2007). This trend reflects increasing awareness of the urgent need to sustainably manage fragile marine areas subject to anthropogenic and natural stresses. Establishing Marine Protected Areas is one strategy to achieve this, but their proper design requires biological and physical knowledge that is not always available (Cowen *et al.*, 2006; Van der Molen *et al.*, 2007). In fact, studies of temporal changes in connectivity that generate knowledge on the life cycle of fish species and their relation with environment changes are very scarce, particularly in tropical and subtropical regions, where the large number of species increase ecosystem complexity.

In the Gulf of California, an ecosystem with numerous Marine Protected Areas and ecological reserves (Fig. 1), some studies of connectivity routes using the three-dimensional nonlinear baroclinic model developed by Marinone (Marinone, 2003) have been made. Calderon-Aguilera *et al.* (Calderon-Aguilera *et al.*, 2003) found that during summer, blue shrimp larvae (*Litopenaeus stylirostris*) in the upper Gulf of California were transported by surface currents from the continental coast to the peninsular coast (east to west), where they were recruited. Marinone *et al.* (Marinone *et al.*, 2008) observed a cyclonic downstream connectivity from spawning areas of rocky-habitat species from the mainland coast to the peninsular coast. Peguero-Icaza *et al.* (Peguero-Icaza *et al.*, 2008) found high retention of

fish larvae in the northern gulf and an export path from north to south following the winter anticyclonic main flow. Cudney-Bueno *et al.* (Cudney-Bueno *et al.*, 2009) found local retention of mollusk larvae in a reserve network, with enhanced recruitment to local fisheries, on the mainland coast of the northern gulf during summer. Although these previous works supported their results on parts of the seasonal circulation, studies addressing seasonal changes in the connectivity routes have not been done.

Seasonal surface circulation in the Gulf is forced mainly by the geostrophic coastal circulation of the eastern tropical Pacific and, to a lesser degree, by surface winds, with a small contribution from buoyancy flux (Beier, 1997; Marinone, 2003). Direct observations of currents (Lagrangian and Eulerian) made by Lavín *et al.* (Lavín *et al.*, 1997) and Palacios-Hernández *et al.* (Palacios-Hernández *et al.*, 2002) and analytical and numerical models (Beier, 1997; Marinone, 2003; Zamudio *et al.*, 2008) have established that the surface circulation in the entire Gulf of California is anticyclonic from late autumn to early spring and cyclonic in summer. An outstanding feature is the eddy-like circulation that dominates the northern gulf, which is cyclonic from June to September and anticyclonic from November to April (Lavín *et al.*, 1997; Lavín and Marinone, 2003; Gutiérrez *et al.*, 2004). The seasonal circulation patterns are very

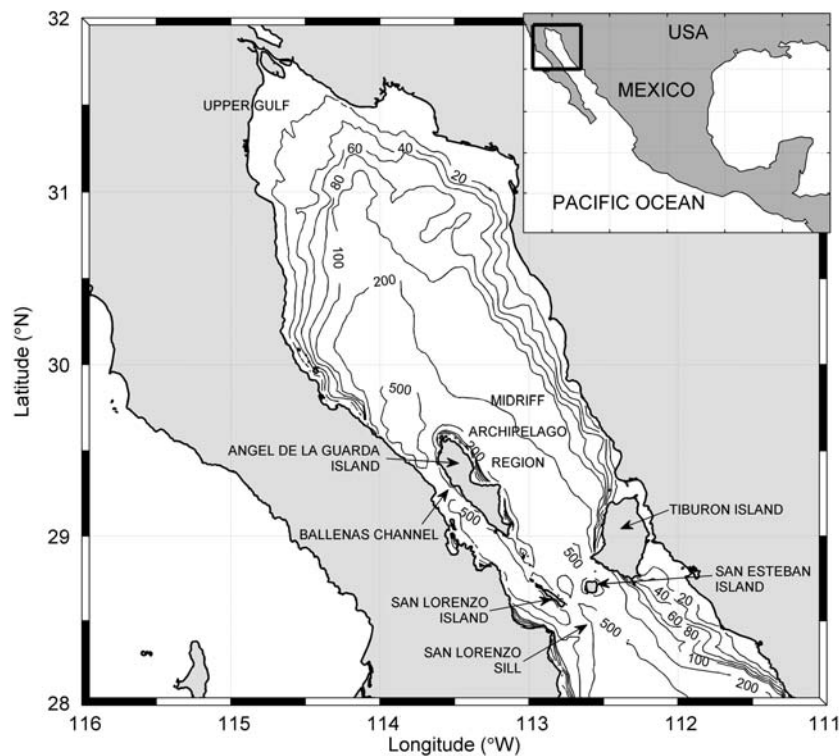


Fig. 1. Bathymetry of the northern Gulf of California (depth in meters), with named places and basins.

energetic because the seasonal forcings by the eastern tropical Pacific coastal current and by the surface winds are in phase (Beier, 1997). In the southern gulf, seasonal currents are dominant, while in the northern gulf their speed is similar to tidal currents, except in shallow bays where tidal currents dominate.

In this context, Sánchez-Velasco *et al.* (Sánchez-Velasco *et al.*, 2009) described the interactions between three larval fish assemblages (Fig. 2) that varied seasonally in species composition and dominance (Table I), in relation to the main characteristics of oceanographic conditions in the Gulf of California (for a review, see Lavín and Marinone, 2003). These biophysical interactions were explained with a conceptual model, which was considered propositional, in part because there was little

knowledge about dispersion routes and connectivity among larval fish assemblage areas in this ecosystem. The conceptual model took into account that during early and high summer, the cyclonic surface circulation includes the eddy in the center of the northern gulf and a northwestward coastal current on the mainland shelf, which is a continuation of an inflowing current from the southern gulf; this current could carry larvae from the southern gulf, and nutrients and biomass from the tidal-mixing area over the sills into the coastal area of the northern gulf. Stratification in summer is strong, the surface mixed layer is shallow (~5 m deep) and very warm (~30°C). Coastal demersal fish species (e.g. *Gobulus crescentalis*, *Lythrypnus dalli*) are dominant in early summer, but are replaced by eastern boundary current species

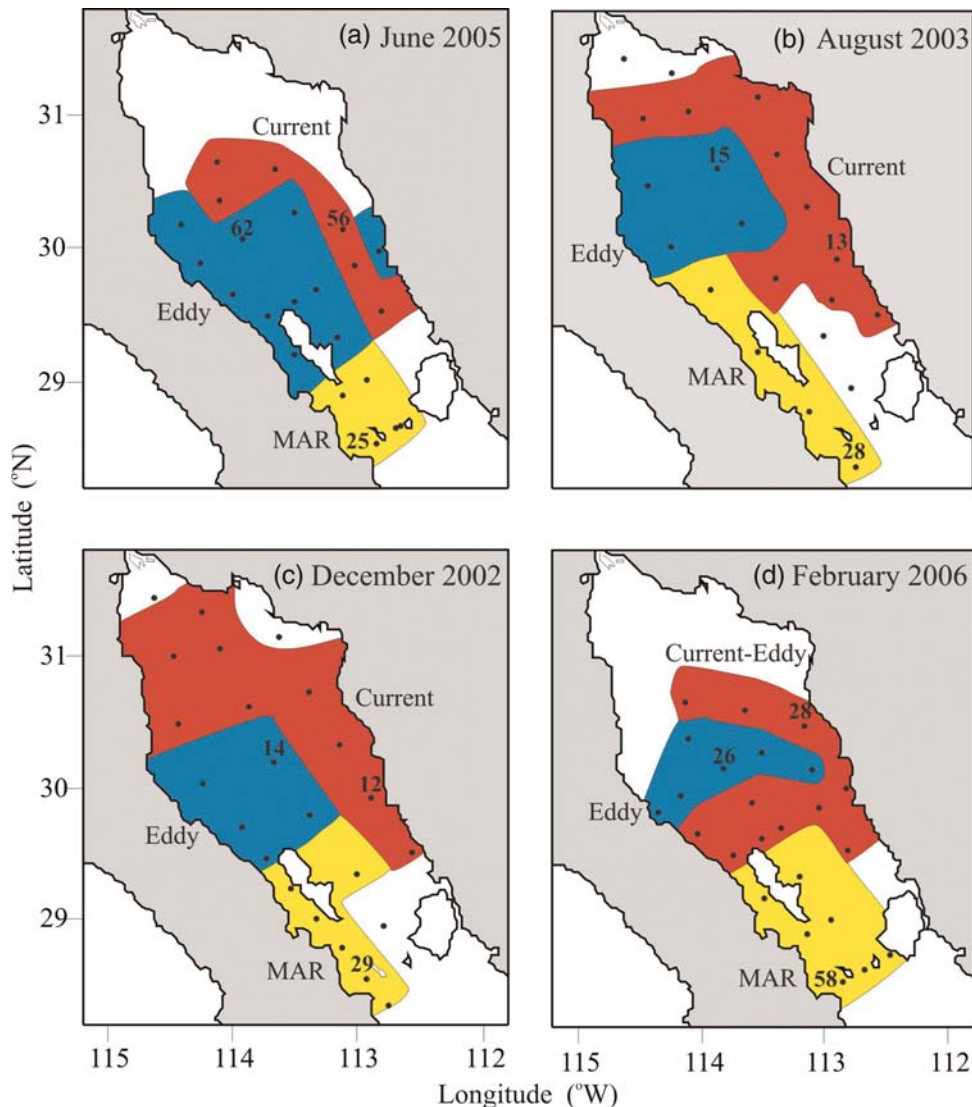


Fig. 2. Location of larval fish assemblages in the northern Gulf of California for (a) June 2005, (b) August 2003, (c) December 2002 and (d) February 2006. Numbered stations are used in Fig. 3. Figure modified from Sánchez-Velasco *et al.* (2009).

Table I: Dominant taxa of the larval fish assemblages defined in the northern Gulf of California by the Olmstead–Tukey test (X is mean abundance; % F is frequency of occurrence)

Dominant taxon	June 2005						August 2003						December 2002						February 2006						
	Current		Eddy		MAR		Current		Eddy		MAR		Current		Eddy		MAR		Current–Eddy		Eddy		MAR		
	X	% F	X	% F	X	% F	X	% F	X	% F	X	% F	X	% F	X	% F	X	% F	X	% F	X	% F	X	% F	
<i>Albula</i> sp.							202	100																	
<i>Anchoa</i> spp.			81	60			491	89	351	100															
<i>Balistes polylepis</i>							202	100																	
<i>Benthoosema panamense</i>	333	86			85	75	1077	89	1731	100	815	100	36	89	138	80	541	100							
<i>Engraulis mordax</i>													190	100	243	100	293	100	1327	100	1279	100	935	100	
<i>Etropus crossotus</i>			47	60																					
<i>Gobulus crescentalis</i>	29	71	51	89																					
<i>Lythrypnus dalli</i>			33	60																					
<i>Merluccius poeductus</i>																					345	80			
<i>Opisthonema libertate</i>							548	100																	
<i>Serranus</i> spp.			24	60																					
<i>Sphyræna ensis</i>			17	40																					
<i>Triphoturus mexicanus</i>	25	43			45	100					68	67													
<i>Xenistius californiensis</i>			21	40																					
Number of taxa	24		29		7		47		13		23		14		11		12		10		8		9		
Number of stations	7		10		4		9		3		4		9		5		6		10		5		7		
Mean larval abundance	516		428		147		3038		2848		1260		275		430		933		1408		1818		1102		

Abundance is expressed as number of larvae per 10 m². Table modified from Sánchez-Velasco *et al.* (2009).

(e.g. *Opisthonema libertate*, *Anchoa* spp.) in high summer. In Ballenas Channel, the dominant fish larvae are mesopelagic (e.g. *Benthoosema panamense*). In contrast, during winter, the eddy is anticyclonic and the coastal current is south-eastward, with an outflow from the northern gulf to the southern gulf. Stratification in winter is weak, the surface mixed layer is deep (~100 m) and cool (~16–17°C) in the eddy and in the shelf, and cold in Ballenas Channel (~14°C). Species richness decreases drastically compared with the summer conditions. Dominant fish larvae species are mesopelagic (e.g. *Benthoosema panamense*) in late autumn, and eastern boundary current species (e.g. *Engraulis mordax*, *Merluccius productus*) in high winter.

The conceptual model assumes that the hydrodynamic processes that characterize seasonal circulation in the Gulf of California generate seasonal routes of connectivity between zooplankton habitats, with effects on fish recruitment. In this article, we extend and give quantitative support to the work of Sánchez-Velasco *et al.* (Sánchez-Velasco *et al.*, 2009) by studying the effect of seasonal circulation on connectivity routes of larval fish assemblages in the Northern Gulf of California, via particle tracking with currents from a 3D numerical model. Implications of seasonal changes in connectivity routes on larval survival and successful recruitment of the dominant species are discussed.

METHODS

This study is based on larval fish assemblages obtained from data collected on four cruises; two representing the anticyclonic phase (December 2002 and February 2006) and two representing the cyclonic phase (August 2003 and June 2005) of seasonal circulation in the Gulf of California, as explained in detail by Sánchez-Velasco *et al.* (Sánchez-Velasco *et al.*, 2009). However, the larval fish data base published in that article has been modified: for the August 2003 cruise, *E. mordax* species was changed to *Anchoa* spp., which is reflected in Table I.

The larval fish assemblages and their areas were defined by canonical correspondence analysis (CCA; Ter Braak, 1986) applied to the data of each cruise. Before calculating the CCA, the standardized fish larvae data were root–root transformed, to reduce the statistical weight of the most abundant species (Field *et al.*, 1982). The matrix of environmental parameters used in the analysis were the top 10 m average values of temperature, salinity and dissolved oxygen, the zooplankton sampling depth and the zooplankton biomass. The results (see Fig. 10 of Sánchez-Velasco *et al.*, 2009) were shown as biplots (the first two ordination axes) with environmental parameters as vectors and eligible

elements (sampling stations) as points in the ordination space (Ter Braak, 1986; De la Cruz-Aguero, 1994).

The resulting groups of sampling stations in each CCA were mapped independently for each cruise. In all cases, three groups of stations were defined, and they corresponded to three environmental regions: (i) the eddy region in the northern gulf, (ii) the Midriff Archipelago Region (MAR) and (iii) the mainland coastal current. Although each group of stations covered different areas related to seasonal environmental changes; they were named “Eddy”, “MAR”, and “Current” for all cruises to simplify description of seasonal evolution of the system in the Results and Discussion section. The exception was the February cruise, when “Current–Eddy” was used instead of “Current” because of its extension (Fig. 2d).

The set of species identified in each group of sampling stations, called a larval fish assemblage, is considered to represent a specific planktonic environment. Some species can be present in various environments because the premise is that, although adult fish can cross planktonic boundaries, their eggs and larvae might be retained (e.g. Espinosa-Fuentes and Flores-Coto, 2004; Sanchez-Velasco *et al.*, 2007; Danell-Jimenez *et al.*, 2009). If the environments are favorable for survival, the larvae would develop in the different environments during their planktonic phase. Since most fish larvae were in pre-flexion, we assume that the planktonic environment with the highest larval abundance was the main spawning area of the species. The dominant species in each assemblage were determined with the Olmstead–Tukey test (Sokal and Rohlf, 1985), which takes into account abundance and relative frequency of each species. The dominant species are considered the representative species of each larval fish assemblage.

To establish connectivity routes between the areas occupied by the larval fish assemblages (Fig. 2) and with the southern gulf, we calculated connectivity matrices by passive-particle tracking. The particle-tracking algorithm used the field of currents from the 3D hydrodynamic baroclinic numerical model of Marinone (Marinone, 2008) and a random-walk scheme to simulate turbulent diffusion; the equations of the model and the 3D advection–diffusion particle-tracking scheme are presented in the Supplementary Material. The particle-tracking time step was 1 h. The outputs of the model were also used to provide a description of the expected seasonal circulation in the Gulf of California at the time of the cruises.

Particles were released at the observation stations (rather than at evenly distributed points), because we wanted to obtain an estimate of the dispersion routes of the larval fish assemblages that were actually observed;

the ecological areas were defined from the data of the sampling stations, not from theoretical considerations. Four hundred passive particles were released at each sampling station, and then tracked for 30 days; releases were made the first day for every sampling month: June 2005, August 2003, December 2002 and February 2006. We assumed that the early life history of the most representative fish species has planktonic larval stages lasting a maximum of 30 days. Connectivity between the areas at a stated time after releasing the particles was quantified by connectivity matrices (Tables II and III), in which the vertical axis represents the release area, and the horizontal axis represents where the particles are found after t days ($t = 15, 30$ days). The values of the elements in the matrices were given as percentages; the main diagonal represents the percentage of the particles that remained in their area of origin after the stated time.

Table II: Connectivity matrices (% of particles released) for June and August corresponding to tracks in Figs 5 and 6, 15 and 30 days after release

	June 2005			August 2003		
	Current	Eddy	MAR	Current	Eddy	MAR
Position after 15 days →						
Current	88	0.7	0	79.6	17.4	0
Eddy	23.9	65.5	9.2	39.3	60.8	0
MAR	21.2	0	59.5	66	0	33.8
Position after 30 days →						
Current	76.4	6.1	0	71.6	21.8	0
Eddy	55.6	40.2	0	23.5	74.1	2.9
MAR	57.9	0.9	9.8	66.2	0.2	33.4

The vertical axis represents the departure area and the horizontal axis represents the arrival area.

Table III: Connectivity matrices (% of particles released) for December and February corresponding to tracks in Figs 7 and 8, 15 and 30 days after release

	December 2002			February 2006		
	Current	Eddy	MAR	Current-Eddy	Eddy	MAR
Position after 15 days →						
Current	11.9	44.9	12.6	30.4	33.6	12.4
Eddy	3.4	75.9	20.4	20.3	40.1	20.8
MAR	0	0.8	28.2	0	0	30.2
Position after 30 days →						
Current	15.4	27.9	23.8	15.5	32.2	9.3
Eddy	20.8	41.4	37.1	28.2	35.8	16.5
MAR	0	2.7	19.8	0	0.2	23.4

The vertical axis represents the departure area and the horizontal axis represents the arrival area.

The velocity field used to calculate the particle trajectories came from the numerical model of Marinone (Marinone, 2008), but with unsmoothed bathymetry and with a finer grid by a factor of three. Also, new bathymetry data from around San Esteban and San Lorenzo islands and from the upper gulf were included. This provided a bathymetry with more realistic deeper sills and basins around the study area. A very brief description of the model is given here and in the Supplementary Material; for more details see Marinone (Marinone, 2003) and references therein. The model is the three-dimensional baroclinic Hamburg Shelf Ocean Model (HAMSOM) developed by Backhaus (Backhaus, 1985) and adapted to the Gulf of California by Marinone (Marinone, 2003). The grid size is $0.833' \times 0.83'$ ($\sim 1.31 \times 1.54$ km) horizontally, and 12 layers in the vertical, with the lower levels fixed at 10, 20, 30, 60, 100, 150, 200, 250, 350, 600, 1000 and 4000 m. At the open boundary, the model was forced with linearly interpolated tidal harmonics (M2, S2, N2, K2, K1, O1, P1, Ssa and Sa) from observations at Mazatlán and Cabo San Lucas (Morales-Perez and Gutierrez-de-Velasco, 1989; Marinone, 2003), and with seasonal climatological hydrography from our historical data base of the Gulf of California. The data consist of 41 cruises from 1939 through 1995 which includes about 2600 casts. From these data, the seasonal signal of temperature and salinity fields was interpolated across the open boundary (Marinone, 2003). At the sea surface, climatological heat and fresh water fluxes were imposed (Marinone, 2003). A space-variable seasonal climatology of wind stress, constructed from the wind data provided by the SeaWinds scatterometer on the QuickSCAT (Quick Scatterometer) satellite, was imposed at the surface (http://podaac.jpl.nasa.gov/DATA_CATALOG/quikscatinfo.html). Although this simplified wind forcing does not include event variability, at the timescale of planktonic larval stage duration, particle displacements due to the seasonal wind signal are much larger than those due to event variability (Peguero-Icaza et al., 2008).

The timescales of the model, determined by the forcing agents, are seasonal and tidal. Validation of the model at the seasonal timescale was made by Marinone (Marinone, 2003), by showing that it adequately reproduces the seasonal signals of surface temperature, heat balance, tidal elevation and the observed seasonally reversing eddy-like surface circulation in the northern Gulf of California. The tidal current ellipses, both barotropic and baroclinic, produced by the model were compared against observations by Marinone and Lavín (Marinone and Lavín, 2005), who found good overall agreement for the semidiurnal constituents (M2 is by far the most important harmonic in the Gulf), while the diurnal were underestimated.

RESULTS AND DISCUSSION

Hydrography and stratification

The seasonal evolution of vertical hydrographic structure in the area of study is shown in Fig. 3, using representative temperature and density profiles from the three larval fish assemblage areas shown in Fig. 2. It is apparent in Fig. 3 that the density profile in the Gulf is controlled by temperature; salinity (not shown) decreases stratification slightly because it diminishes downward (Lavín and Marinone, 2003). Only the top 200 m of the temperature and density profiles are

shown. In the Eddy area (Figs 3a and b), the surface temperature changed from $\sim 22.5^{\circ}\text{C}$ to $\sim 30^{\circ}\text{C}$ between June and August and stratification increased sharply. In summer (June and August), the surface mixed layer was only a few meters deep; by December, the mixed layer deepened to ~ 50 m and cooled to $\sim 21^{\circ}\text{C}$ and by February to ~ 80 m and $\sim 17^{\circ}\text{C}$, respectively. Over the mainland shelf (Current area), temperature and stratification increased in the entire water column between June and August (Figs 3c and d), and then decreased steadily in December and February. The MAR temperature profiles (Figs 3e and f) show that

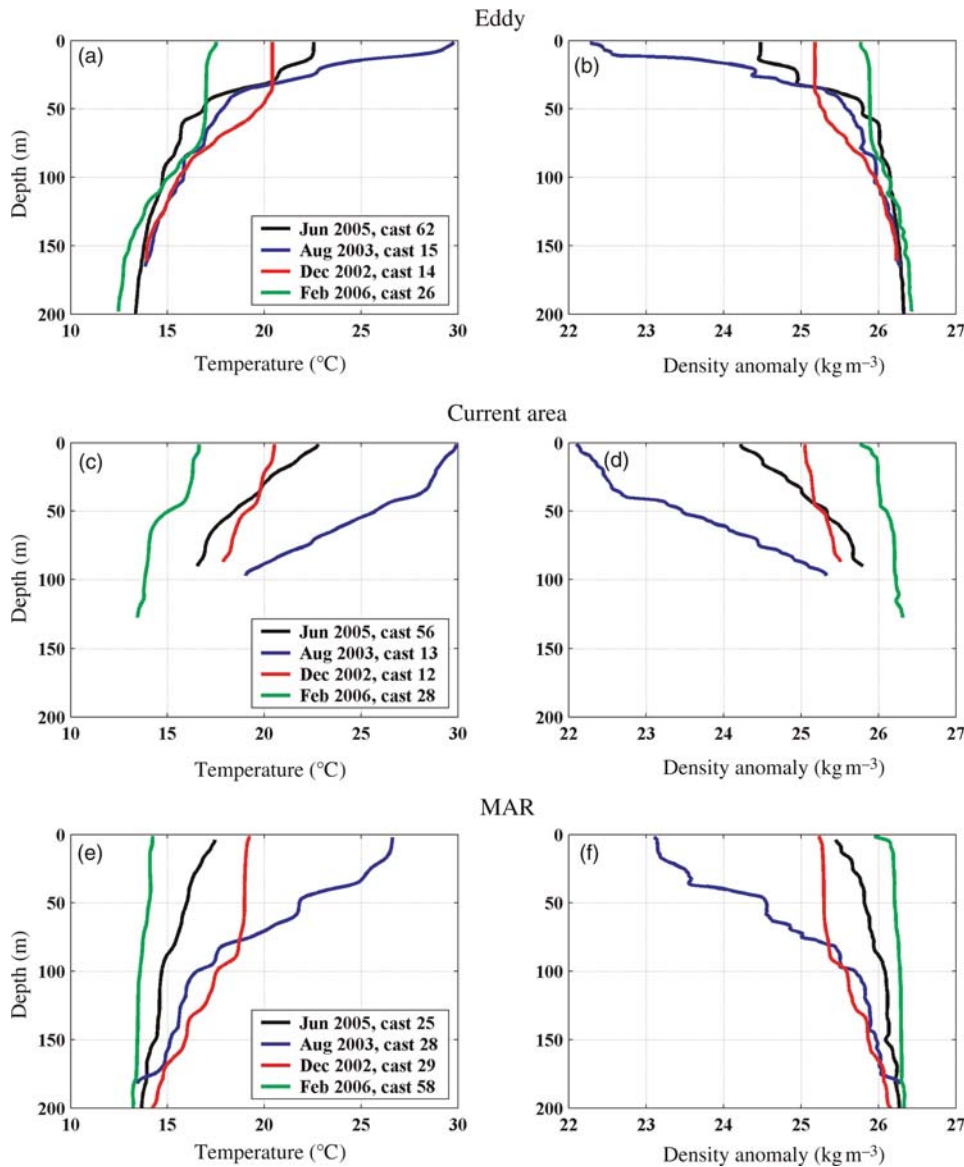


Fig. 3. Seasonal evolution of the vertical hydrographic structure (top 200 m) in the areas of the northern Gulf of California marked in Fig. 2. (a) Temperature and (b) density profiles from the Eddy area, (c) temperature and (d) density profiles from the Current area (mainland shelf), and (e) temperature and (f) density profiles from the midriff archipelago region (MAR area).

stratification in the upper 100 m was significant only in August, with maximum surface temperature $\sim 27^{\circ}\text{C}$, some 3°C cooler than in the other two provinces. In February, the upper 200 m were well mixed. The striking dissimilarity of the hydrography in the MAR with the other areas results from intense tidal mixing (Argote *et al.*, 1995) and continuous convergence-induced upwelling imposed by the thermohaline circulation of the Gulf (López *et al.*, 2006).

Circulation

The monthly average surface circulation predicted by the numerical model (Marinone, 2003, 2008), shown in Fig. 4, is in agreement with the observations of seasonal circulation (Lavín *et al.*, 1997; Carrillo *et al.*, 2002; Palacios-Hernández *et al.*, 2002). For June (Fig. 4a), the cyclonic flow dominates circulation, the northwestward coastal current on the mainland side is faster than the southeastward flow on the peninsular side; this is the early part of the cyclonic phase. The strongest currents were found where sills were present in the channels between the islands. The prediction of the model for

August (Fig. 4b) shows that the circulation pattern is similar to the currents in June but stronger. A cyclonic eddy occurred in both months in the center of the northern Gulf of California, which was better defined during the mature phase of cyclonic circulation (August).

In December (Fig. 4c), anticyclonic circulation covered the northern Gulf of California. The fastest currents were again found on the mainland shelf, but now the coastal current flows out of the northern gulf. The model predictions for February (Fig. 4d) have a circulation similar to December but less intense in general. The central anticyclonic eddy was better defined in February than in December.

Figure 3 shows that stratification is always present in the upper layers of the Gulf of California (except in Ballenas Channel during winter), and that it exhibits a seasonal variability with a maximum in summer and minimum in winter. The 3D model includes spatial and temporal variations in stratification and, being baroclinic, takes full account of the effect of stratification on circulation. The presence of stratification causes vertical shear of the horizontal currents and even direction reversal with depth. This has consequences

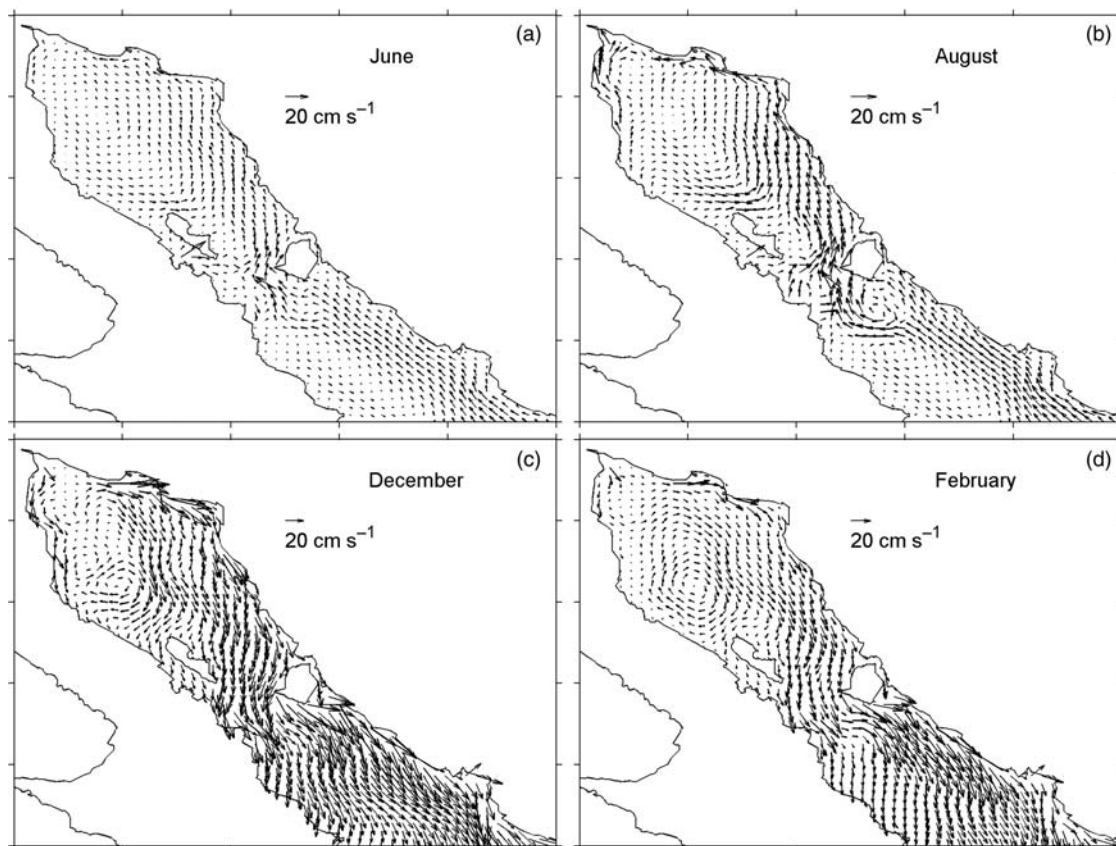


Fig. 4. Monthly mean surface currents (0–10 m) in the northern Gulf of California obtained from the 3D numerical model of Marinone (2003): (a) June 2005, (b) August 2003, (c) December 2002 and (d) February 2006. For clarity, only one in every 11 vectors is shown.

for the tracking of particles. Since they are also advected by the vertical component of the velocity field (Marinone *et al.*, 2008), they are subjected to different velocities as they change depth. Particles subjected to 3D advection–diffusion follow trajectories that can be very different from those of particles that remain in the surface layer (Marinone, 2006). However, for particles released in the northern gulf, the mean depth of the maximum vertical excursions obtained by the numerical model after 1 month of tracking is only 30–50 m (Marinone, 2006), which means that particles released at the surface will remain in the upper layers. Therefore, these results can be considered the connectivity among surface assemblages, which is a good approximation because most fish larvae concentrate in the upper layers, especially above the thermocline (Sánchez-Velasco *et al.*, 2007; Danell-Jiménez *et al.*, 2009).

One of the limitations of the numerical model is that it produces a seasonal climatological circulation, with little change from year to year. According to Lavín *et al.* (Lavín *et al.*, 2003), the interannual anomalies of the Gulf are strongly correlated with the Southern Oscillation Index (SOI). Since there were no strong interannual events during our period of sampling, we assume that the results describe conditions when the seasonal timescale dominated the general circulation in the Gulf.

Connectivity and dispersion routes

The connectivity routes revealed by particle tracking are shown in Figs 5–8 and are described below in a seasonal sequence. The trajectories in these diagrams include tidal advection ellipses. The particles main trajectories are dominated by residual flows, while tidal currents only make the trajectories oscillate, with loops the size of the tidal excursion (~5–8 km) stretched along the general path determined by the large-scale circulation. This means that, at the timescale on which we are focusing (15–30 days), tidal currents are less relevant to connectivity than the residual currents (Marinone *et al.*, 2008; Peguero-Icaza *et al.*, 2008). The timescale was determined by the duration of the larval stage of the most important species in the assemblages; *Benthoosema panamense*, *Engraulis mordax* and other abundant species have larval periods longer than 2 weeks (Moser, 1996).

Early cyclonic phase

During June, the early cyclonic phase, the strong coastal current was present and high temperature and stratification (Fig. 3a) favored phytoplankton blooms (Lavín and

Marinone, 2003; Hidalgo-González and Alvarez-Borrego, 2004). In this season, the Current, Eddy and MAR assemblages were well defined, with a large Eddy assemblage area (Fig. 2a) and many dominant species (Table I). The tracks of the particles released at each station are shown in Fig. 5. For the first 15 days, the particles from the Current assemblage area on the mainland side showed northward displacement (Fig. 5a), and 88% remained in the assemblage area (Table II). The particles from the Eddy assemblage area moved south, except those released north of Angel de la Guarda Island, which moved east (Fig. 5c); retention in the area was 65% (Table II). Some particles released in the MAR assemblage area (Fig. 5e) were trapped by an eddy over San Lorenzo sill, which could be caused by the tidal-mixing front that is found there (Argote *et al.*, 1995; Danell-Jiménez *et al.*, 2009); some particles were carried eastward and then northward when they entered the Current assemblage area and were carried by the coastal current. This assemblage showed 59% particle retention (Table II). After 30 days (Fig. 5b, d and f), the effect of the cyclonic circulation was more evident; the tracks of particles from the Current and Eddy assemblages described the central eddy and the particles from the MAR assemblage were carried northward by the coastal current on the mainland shelf. After 30 days of tracking, more than 55% of the particles of the Eddy and MAR assemblages were found in the Current assemblage area (Table II). This high connectivity among assemblages after 30 days indicates that hydrodynamic boundaries of the assemblages were weak compared with the mature phase (August), described below.

The main dispersion route during the early cyclonic phase is toward the northwestward coastal current on the mainland side. This resulted in 80% of the total of particles remaining inside the study area. This proportion would be higher if we considered the particles that drifted toward the upper gulf. Figures 5e and 5f support the proposal of Sánchez-Velasco *et al.* (Sánchez-Velasco *et al.*, 2009) that nutrients and other properties from the MAR tidal-mixing area are transported to the mainland shelf during the cyclonic phase. The main dispersion route may explain why the Current larval fish assemblage area in the conceptual model described by Sánchez-Velasco *et al.* (Sánchez-Velasco *et al.*, 2009) showed a high level of primary productivity, zooplankton biomass and abundance of larval fish. On the other hand, the MAR assemblage area showed low values of these parameters, which result from cool conditions created by vertical mixing and high particle dispersion.

Since the dominant species during this phase was *B. panamense* (mesopelagic) in the Current and MAR

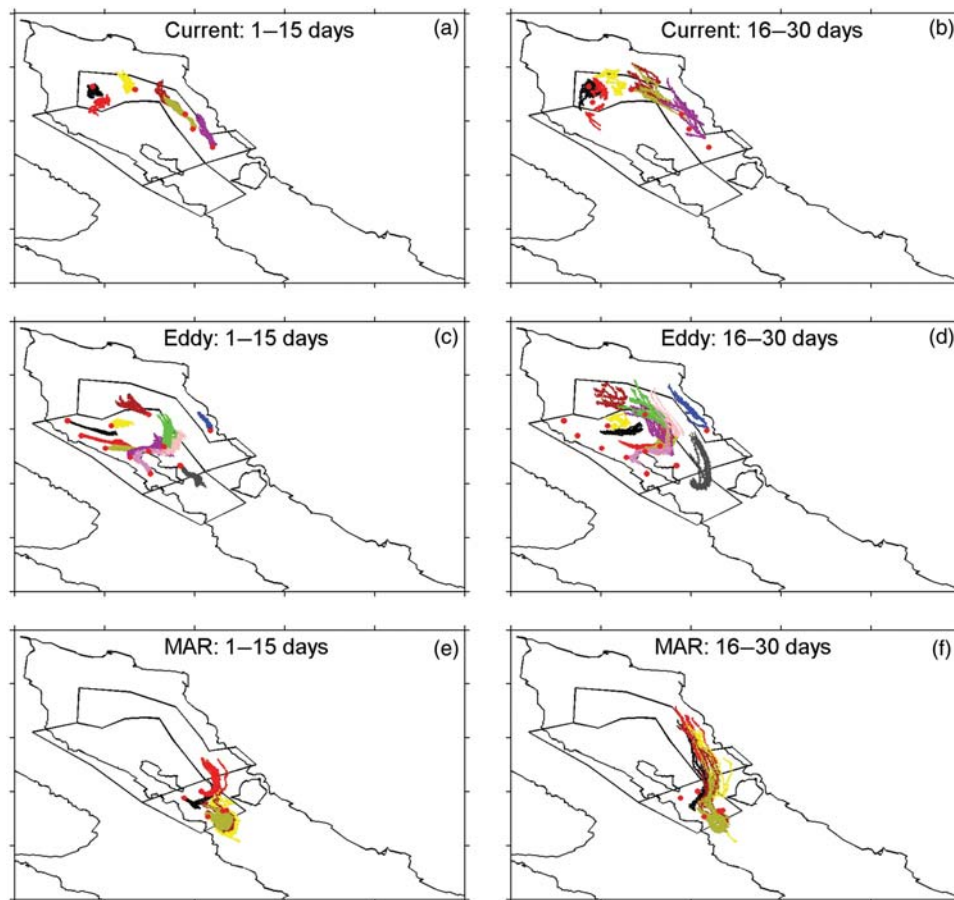


Fig. 5. Trajectories of particles released at the stations of the different larval fish assemblages for June, calculated from the 3D current fields produced by the numerical model. **(a)** Current for days 1–15, **(b)** Current for days 16–30, **(c)** Eddy for days 1–15, **(d)** Eddy for days 16–30, and **(e)** MAR for days 1–15, **(f)** MAR for days 16–30. For clarity, only the tracks of every 10th particle out of 400 released at each station are shown. Particle positions were plotted every hour.

assemblages and coastal-demersal species, such as *G. crescentalis*, *Etropus crossotus* and *L. dalli* dominated the Eddy assemblage (Table I), we suggest that most of the spawning product from these species remained near the spawning areas for at least the first 15 days. After 30 days, larvae of these species concentrated in the Current assemblage area and showed low dispersion into the southern gulf. Therefore, most of the dominant species spawning in the northern Gulf during the early cyclonic period would probably be recruited there.

Mature cyclonic phase

In August, the cyclonic eddy was well established (Sánchez-Velasco *et al.*, 2009), indicating mature cyclonic phase conditions. Stratification was stronger than in June (Fig. 3). The highest zooplankton biomass and species richness of the annual cycle occurred in this period (Sánchez-Velasco *et al.*, 2009). The three

assemblages (Current, Eddy and MAR) were also defined in August and the Eddy assemblage area was well defined in the center of the northern gulf (Fig. 2b). In the first 15 days, particles from the Current area showed rapid northward displacement (Fig. 6a) and 79% of them remained inside the assemblage area (Table II). In the Eddy area, particles were trapped by the cyclonic eddy circulation (Fig. 6c), with retention of 60% (Table II); of the particles from the MAR assemblage, 66% were transferred to the Current area, while the rest remained trapped against the coast in the channel (Fig. 6e). After 30 days (Figs 6b, d and f), trapping was more evident in all the assemblages (Table II), with >70% of the particles still remaining inside the assemblage areas (except for MAR, where 66% of its particles drifted into the Current area). The highest retention occurred in the cyclonic eddy area (74%). This high retention suggests that hydrodynamic boundaries of assemblages were more stable in August than in

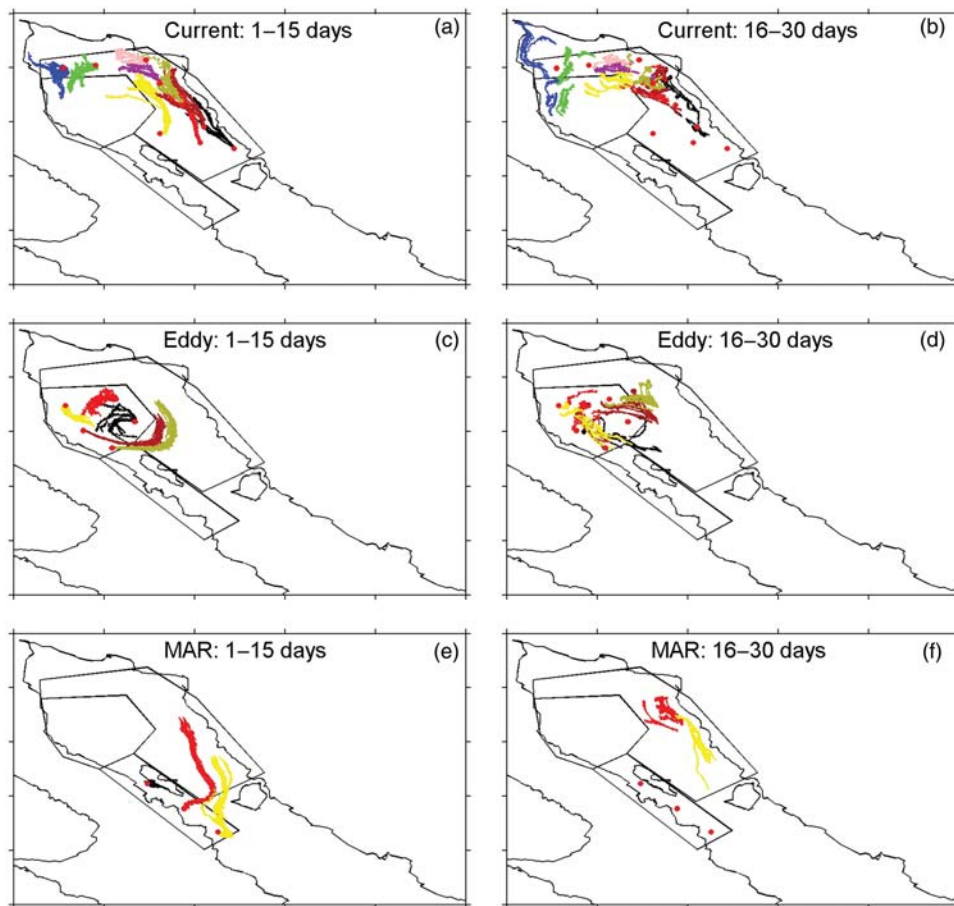


Fig. 6. Trajectories of particles released at the stations of the different larval fish assemblages for August, calculated from the 3D current fields produced by the numerical model. **(a)** Current for days 1–15, **(b)** Current for days 16–30, **(c)** Eddy for days 1–15, **(d)** Eddy for days 16–30 and **(e)** MAR for days 1–15, **(f)** MAR for days 16–30. For clarity, only the tracks of every 10th particle out of 400 released at each station are shown. Particle positions were plotted every hour.

June, as the cyclonic phase matured. The remaining particles (25–30%) followed the dispersion route establishing connectivity from MAR toward Current and from there to Eddy, where they were trapped by the cyclonic eddy. This period was the most retentive, with 98% of the total of particles remaining inside the assemblage areas.

The dispersion route in the mature cyclonic phase changed from concentrating particles in the coastal current during the early cyclonic phase (June) to two consecutive scenarios: a dispersion route that concentrated the particles in the coastal zone during the first 15 days (Current assemblage), and another that concentrated the particles in the eddy in the second 15 days. This change in the dispersion route coincides with the change of dominant species from June to August (Table I), as described in the conceptual model (Sánchez-Velasco *et al.*, 2009), where the coastal–demersal species were replaced by massive spawning by

coastal–epipelagic species, such as *Opisthonema libertate*, and *Anchoa* spp., although *B. panamense* remained a dominant species in the entire northern Gulf of California. The first scenario, which explains that >50% of the particles concentrated in the coastal current area, could correspond to the coastal–epipelagic species that were dominant in the Current assemblage area, which is a shallow region. According to Landaeta (Landaeta, personal communication) epipelagic fish larvae can change their position in the water column by means of their gas bladder, which could lead to decreased dispersion of these species. This could be extrapolated to coastal–epipelagic species in the Gulf that remained in the coast areas. In addition, strong stratification with an evident pycnocline (Fig. 3a) could favor retention at the coast of this type of larvae (Sánchez-Velasco *et al.*, 2007). The second scenario applies to mesopelagic fish such as *B. panamense* and *Triphoturus mexicanus* which could feed near the coast and

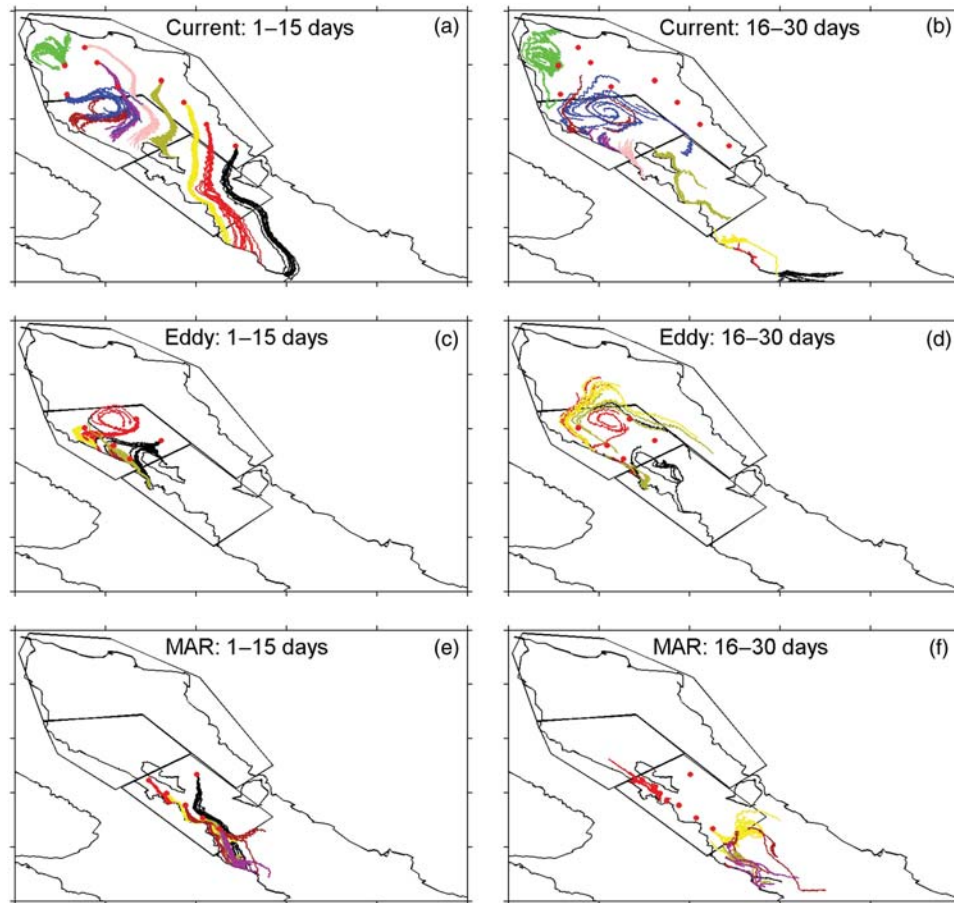


Fig. 7. Trajectories of particles released at the stations of the different larval fish assemblages for December, calculated from the 3D current fields produced by the numerical model. **(a)** Current for days 1–15, **(b)** Current for days 16–30, **(c)** Eddy for days 1–15, **(d)** Eddy for days 16–30 and **(e)** MAR for days 1–15, **(f)** MAR for days 16–30. For clarity, only the tracks of every 10th particle out of 400 released at each station are shown. Particle positions were plotted every hour.

then be recruited in the central eddy area. The abundance of *B. panamense* can be an indicator of this dispersion route; although it spawned throughout the study area, its highest abundance occurred in the Eddy area. Again, the dispersion route during the mature cyclonic period resulted in low abundance of larvae in the MAR assemblage area. The lowest connectivity between the northern and southern part of the MAR occurred during the mature cyclonic phase; this could have significant consequences for the Gulf of California ecosystem.

Early anticyclonic phase

In December, the early anticyclonic phase, Current, Eddy and MAR larval fish assemblages were well defined again (Fig. 2c). At this time, the environment was changing rapidly, with a tendency to spatial homogenization. The currents during this phase were the

strongest (Fig. 4c). Vertical mixing by strong winter northwesterly winds and cooling-induced convection created a surface mixed layer that reached a depth of at least 50 m (Fig. 3c). These environmental changes were reflected in the tracks during the first 15 days (Figs 7a, c and e), where particles from two of the assemblages were dispersed; only those from the Eddy assemblage showed high retention (76%) (Table III). The particles released in the Current and MAR assemblage areas had rapid southeastward displacement, which explains the low retention in these areas (12 and 28%, respectively). Of the particles released in the Current area, 45% were carried to the Eddy area, stressing the significant role of the eddy on larval retention. The particles released in the Eddy area were affected by the anticyclonic circulation, most of them remaining in the area; some particles moved southward and entered Ballenas Channel, where they were stranded near the coast. After 30 days (Figs 7b, d and f), more than 30% of the

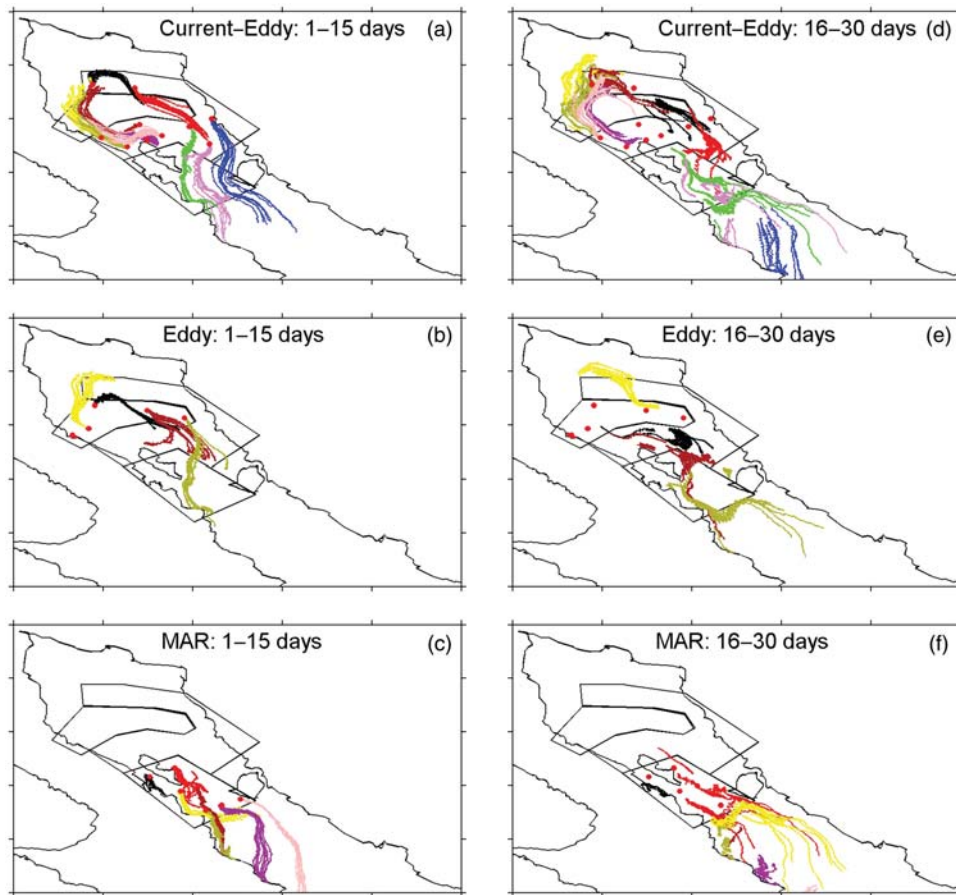


Fig. 8. Trajectories of particles released at the stations of the different larval fish assemblages for February, calculated from the 3D current fields produced by the numerical model. (a) Current–Eddy for days 1–15, (b) Current–Eddy for days 16–30, (c) Eddy for days 1–15, (d) Eddy for days 16–30 and (e) MAR for days 1–15, (f) MAR for days 16–30. For clarity, only the tracks of every 10th particle out of 400 released at each station are shown. Particle positions are plotted every hour.

particles had left the study area. The effect of the circulation pattern became more apparent: the highest retention (41%) occurred in the Eddy assemblage area and the lowest retention occurred in the other two areas. Of the particles from the Current area, 28% remained in the Eddy assemblage area (Table III).

The flow toward the southeast of the coastal current over the mainland shelf generated the dispersion route southward, a drastic change with respect to the cyclonic phase of the circulation (June and August). This dispersion route generated connectivity from Current and Eddy areas to the MAR area; after 30 days, >30% of the particles were outside the study area (Table III). This coincided with a drastic decline of zooplankton biomass, abundance of larval fish and species richness in the northern gulf, which was recorded by Peguero-Icaza *et al.* (Peguero-Icaza *et al.*, 2008) and Sánchez-Velasco *et al.* (Sánchez-Velasco *et al.*, 2009).

The species that dominated during this season were *B. panamense* and *E. mordax* (Table I). Like *B. panamense*, *E. mordax* is a species with a wide distribution in the gulf and adapts to environmental changes (Cotero-Altamirano and Green-Ruiz, 1997; Green-Ruiz and Hinojosa-Corona, 1997; Sánchez-Velasco *et al.*, 2000). The southward dispersion does not limit the survival of the early life stages of either species, because environmental conditions south of the MAR are favorable for their development (e.g. Green-Ruiz and Hinojosa-Corona, 1997; Avalos-García *et al.*, 2003). Particle retention in the anticyclonic eddy area, although lower than in the mature anticyclonic phase, partially explains the high abundance of larvae of both species in the Eddy assemblage area (Table I), compared with the other assemblages. This may occur not only from retention by the eddy, but also because adults preferentially spawn in deep oceanic areas (Avalos-García *et al.*, 2003; Sánchez-Velasco *et al.*, 2009).

Mature anticyclonic phase

In the mature anticyclonic phase (February), the assemblages show different extensions, mainly the one called Current–Eddy, which tended to surround the Eddy assemblage (Fig. 2d). During this period, the central eddy and the southward coastal current off the mainland shelf were well established and the mixed layer reached its maximum depth (Fig. 3). In February, the paths were similar to those in December, but retention was higher (30–40%) during the first 15 days in all the three areas (Table III), and the tracks showed the anticyclonic circulation better (Figs 8a, c and e). Some particles from all the assemblages showed fast southeastward displacement by the coastal current, while particles in the Eddy area show the anticyclonic path; the connectivity from Current to Eddy (34%) continued as in December. After 30 days (Figs 8b, d and f), these paths remained, and more than 40% of the particles were transported from the study area to the south. Retention diminished: Current–Eddy and MAR with 15 and 23%, respectively, and the Eddy assemblage with 36%. Of the particles that dispersed from the Current–Eddy assemblage, 32% joined the Eddy assemblage area (Table III).

Transport of particles to the south, together with the less favorable environmental conditions (deepest and coolest surface mixed layer, Fig. 3) in this phase of the seasonal cycle, can explain the drastic reduction in species richness and almost exclusive dominance of eastern boundary current species (Sánchez-Velasco *et al.*, 2009): *E. mordax* with the highest abundance in the Current–Eddy assemblage area and co-dominance only with *M. productus* in the Eddy assemblage (Table I).

Dispersion routes in this mature anticyclonic phase, like in the mature cyclonic phase, show two scenarios: (i) flow toward the south in the first 15 days, following the coastal current direction, which generated connectivity from the Current–Eddy and Eddy areas to the MAR area; and (ii) concentration of particles in the anticyclonic eddy region in the second 15 days through the connectivity between the Current–Eddy area and the Eddy area (two-way exchange of particles). The first scenario can be related to the extensive distribution of *E. mordax*, a species that could be widely dispersed from the spawning area because it is tolerant of strong environmental changes during its early life stages (Avalos-García *et al.*, 2003). The second scenario can be associated with dominance of *M. productus* (an eastern boundary current species) in the Eddy area. This species was only found in the Eddy assemblage (Table I), probably from almost exclusive spawning in the Eddy area and the high retentively.

General applications for the management of ecosystems

This is the first study relating seasonal evolution of dispersion routes of passive particles and a seasonal ecological model (Sánchez-Velasco *et al.*, 2009) based on the distribution of larval fish assemblages in the northern Gulf of California. This study covered a larger area in the northern gulf than previous studies that used particle tracking as an approximation for transport of larvae in the region, most of which (Calderón-Aguilera *et al.*, 2003; Cudney-Bueno *et al.*, 2009; Marinone *et al.*, 2008) focused on the mainland side and only during the summer (cyclonic period). As a consequence, they reported that the main dispersion route was to the northwest. In studying a larger area, we found two scenarios for summer: a dispersion route that concentrated the particles on the mainland continental shelf (Current assemblage) during the first 15 days after release, in agreement with previous studies, followed by another dispersion path that concentrated the particles in the cyclonic eddy (Eddy assemblage) during the second 15 days.

Peguero-Icaza *et al.* (Peguero-Icaza *et al.*, 2008) found a dispersion route to the southeast, on the mainland shelf of the northern gulf during late autumn. This route is also presented here for the first 15 days after release, and we show that it is followed by a winter scenario (mature anticyclone period), which concentrated particles in the anticyclonic eddy (Eddy assemblage) in the second 15 days.

This comparison between previous studies and our results shows that ecological models that are closer to the dynamics of the ecosystem require studies of particle dispersion around the area of study (e.g. Marine Protected Areas) at spatial scales corresponding to the area covered by the main hydrographic/circulation structures that affect the region. Very often, studies supporting the establishment of Marine Protected Areas are restricted to their immediate surroundings, without considering the larger oceanographic processes that affect them.

In addition, the relationships between the connectivity routes and the seasonal variations show the need to consider seasonal variations of ocean dynamics in the management plans of Marine Protected Areas. This applies to the Gulf of California and other marine ecosystems. For example, in the Irish Sea, Van der Molen *et al.* (Van der Molen *et al.*, 2007) studied dispersal patterns of eggs and larvae of species that spawned just before the spring onset of stratification and found that they typically remained relatively close to their spawning grounds (within ~160 km). These results are similar

to ours during the cyclonic circulation phase of the northern gulf, when the coastal current favors transport toward the eddy, which functions as a retentive structure that favors recruitment in the spawning grounds. However, in the northern gulf and in the Irish Sea, circulation changes seasonally (Horsburgh *et al.*, 2000; Lavín and Marinone, 2003), therefore it is expected that recruitment for most of the species that spawn under other dynamical conditions would necessarily be different; as shown for the anticyclonic circulation phase in the gulf.

The results of our research have important implications for understanding seasonal zooplankton connectivity, and therefore survival of larvae and successful recruitment, in the Gulf of California. Seasonal-change studies can be applied to other marine ecosystems where protection of marine areas is a priority. Considering dynamic temporal variations in the management plans could improve ecosystem protection measures. For a longer perspective, it is desirable to predict, for example, the impact of interannual variability and of climatic change on larval connectivity routes.

CONCLUSIONS

This study showed strong seasonal differences in the connectivity routes for larval fish assemblage areas in the northern Gulf of California. These changes relate to circulation phases (cyclonic and anticyclonic). These seasonal changes also affect connectivity between the northern and the southern part of the gulf, which has important implications for management and conservation of marine protected areas.

In the cyclonic phase (June and August), when the cyclonic eddy and the northwestward coastal current on the mainland shelf were present, particle retention among larval fish assemblages after 30 days was high (>55%), while southward export of particles from the northern gulf to the southern gulf was very small (3–17%). This suggests that larvae of most of the fish species that inhabit the northern gulf are retained near their spawning areas: in June, coastal-demersal species such as *Gobulus crescentalis*, *Etopus crossotus* and *Lythrypnus dalli*, and in August, coastal-epipelagic species and species with extensive spawning such as *Opisthonema libertate* and *Anchoa* spp.

In contrast, in the anticyclonic phase (December and February), when the circulation is anticyclonic and the coastal current over the mainland shelf flows southward, particle retention among larval fish assemblages is low (<35%); transport of particles from the northern gulf to the southern gulf is high (>50%). Hence, recruitment

could occur far from the spawning locations, that is, in the southern gulf. This connectivity route is congruent with the wide spatial distribution and environmental adaptability of *Engraulis mordax* (coastal-epipelagic) and *Benthoema panamense* (mesopelagic) larvae, which are recruited in the open sea. The exception was *Merluccius productus*, which was retained in the Eddy area in February, when the anticyclonic eddy was well established.

Observed seasonal changes in connectivity show that ocean dynamics must be considered in the design of management plans and conservation measures in marine reserves, especially in regions that are exploited by intense fisheries and are under anthropogenic stress.

SUPPLEMENTARY DATA

Supplementary data can be found online at <http://plankt.oxfordjournals.org>.

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